The Ecology of Pelagic Amphipoda, I

Species Accounts, Vertical Zonation and Migration of Amphipoda from the Waters off Southern California

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A SERIES of midwater trawls in the waters off the coast of southern California has revealed large numbers of pelagic amphipods. A sampling program employing an Issacs-Kidd Midwater Trawl (Issacs and Kidd, 1953: 1–21) was conducted in the waters of the Outer Santa Barbara Passage, in the area of the Santa Catalina Basin.

The purposes of this study were (1) to determine the constituents of the local pelagic amphipod fauna, (2) to examine the vertical distributional and migrational patterns of the abundant species, and (3) to analyze some of the hydrographic conditions of the study area and relate this information to the ecology of the amphipods.

This is the first in a planned series of papers. In view of the forthcoming works, such data as size distributions, reproductive conditions, and density fluctuations are omitted from this present paper.

All of the collections considered in this study were obtained through the use of the R/V "Velero IV" of the Allan Hancock Foundation, University of Southern California. Partial support for this work was furnished by grants from the National Science Foundation (G-10691 and G-23467).

METHODS AND MATERIALS

An Issacs-Kidd Midwater Trawl (IKMWT) with a 10 × 10-ft fishing aperture was used in all collections discussed here. A few samples were taken with a Foxton closing device attached to the IKMWT. The Foxton device not only takes a sample at a prescribed fishing depth but retains, separately, the material collected as the trawl is being lowered and raised. Only partial success was attained with this device.

Horizontal tows were taken, and fishing depths were determined through the use of a pressure depth gauge and by triangulation. Although these two methods yielded comparable measurements, the fishing depths recorded here may present some error. The pressure gauge records only the greatest depth to which the trawl descends, and it is the opinion of this author and other workers (Aron et al., 1964:324–333) that the fishing depth of the IKMWT fluctuates while it is being towed. Most of the trawls were conducted for 2-hour periods.

Of the 82 samples used in this study, 58 were quantitatively analyzed by converting counts made in pint aliquots to numbers per hour trawling time. Total counts presented in this paper indicate the number of individuals sorted from these pint aliquots. Although the recorded numbers per trawl hour probably are not precise, they are used at times to offer comparative values of relative population densities at various depths. The qualitative samples were used to determine presence or absence of species at particular times and depths. Table 1 is a record of the day and night hauls taken at various depths. Complete station data and individual sample analyses are on file with the author.

HYDROGRAPHY OF THE STUDY AREA

The continental shelf off the coast of southern California is a complex series of basins, troughs, and islands. It has been termed a continental borderland (Shepard and Emery, 1941:9) due to the striking differences between its topography and that of typical shelf areas. Emery (1960:32–61) offered a detailed description of this region.

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TABLE 1

Depth Distribution of Day and Night Samples Taken in the Outer Santa Barbara Passage

Depth in meters	No. quantitative samples	No. qualitative samples	Total no. samples
Night			
0–50	2	2	4
50–100	2	0	2
100–200	5	2	7
200–300	3	1	4
300–400	4	2	6
400–500	2	0	2
500–600	4	3	7
600–700	2	0	2
700–800	1	0	1
800–900	0	1	1
900–1100	1	2	3
Day			
0–50	0	2	2
50–100	0	2	2
100–200	0	2	2
200–300	3	1	4
300–400	3	1	4
400–500	4	1	5
500–600	5	0	5
600–700	3	1	4
700–800	3	0	3
800–900	4	0	4
900–1100	7	1	8

Certain hydrographic data were utilized in determining the effects of oceanographic conditions on the habits of the pelagic amphipods. Some of this information was obtained from data collected from four stations in the Outer Santa Barbara Passage occupied by the California Cooperative Fisheries Investigations (CCOFI) research vessel. In addition to the CCOFI reports, several bathythermograph readings were taken from the "Velero IV" at times of biological collecting.

From the information gathered, Table 2 was constructed to illustrate the variation in thermocline depth and intensity throughout the year.

Although fluctuations in surface water salinities were noted in the CCOFI reports, there was no indication that the halocline had any effect on the vertical distribution of the amphipods.

The identification of water masses off the southern California coast is difficult due to the great amount of mixing and the formation of complex eddy systems as the California Current passes Point Conception. Emery (1960: 97–115) presented a description of the currents of the local shelf waters and suggested that a zone of mixing between the northern water of the California Current and a deeper layer of southern water exists at depths of from 200 to 300 m. Analysis of temperature-salinity diagrams drawn from the CCOFI data suggests the possibility that the water of the Outer Santa Barbara Passage below about 100 m is an area of mixing of east and west North Central Pacific water. In some cases T-S values approach readings indicative of Pacific equatorial water. These measurements may reflect the incorporation of southern water as the eddy systems turn northward below Point Conception. The surface waters are subject to a great deal of seasonal variation, especially in temperature. The surface salinity values (above 100 m) are typical of those reported as Pacific subarctic water. This top 100 m may be subarctic water which has been heated by solar radiation with very little salinity change as it is brought into lower latitudes by the California Current.

SPECIES ACCOUNTS

Suborder GAMMARIDEA

Family EUSIRIDAE

Rhachotropis natator (Holmes)

Gracilipes natator Holmes, 1908: 527–529, figs. 32–34; Thorsteinson, 1941: 85, pl. 6, figs. 67–70.

Rhachotropis natator Barnard, J. L., 1954*a*: 54–56, pl. 6.

This species occurred in 15 samples taken in this study at depths of 600 to 1100 m. A total of 77 individuals was recorded in quantitative samples. Table 3 illustrates the day and night distributions of this species and shows some evidence of vertical movement. The population appeared to be of about uniform density during the daylight hours between 600 and 1100 m, but during the night captures were made only at depths greater than 900 m. Indicated here is a movement into shallower water dur-

TABLE 2

GENERAL SEASONAL VARIATIONS IN SURFACE TEMPERATURE AND THERMOCLINE DEPTH AND INTENSITY IN THE OUTER SANTA BARBARA PASSAGE

MONTH	SURFACE T°C	DEPTH OF THERMOCLINE MIDPOINT	T°C CHANGE IN TOP 40 METERS
January	14.00	absent	less than 1
February	13.80	absent	less than 1
March	14.50	20 m	3.0
April	14.00	15 m	3.0
May	17.50	25 m	4.5
June	18.00	20 m	5.0
July	19.00	no data	no data
August	21.00	18 m	8.3
September	21.10	27 m	5.1
October	20.10	25 m	4.0
November	16.85	25 m	5.3
December	15.00	absent	1.3

ing the day. The factors influencing this type of deep-water migration are not clear. The absence of perceivable light and the relative constancy of temperatures exclude these factors as being important at such great depths. The vertical movement of *Rhachotropis natator* may, in fact, represent an endogenous rhythm and thus be independent of the environmental conditions.

Family LYSIANASSIDAE

Eurythenes obesus (Chevreux)

Katius obesus Chevreux, 1905: 1–5, figs. 1–3; Stephensen, 1925: 126–127; Schellenberg, 1926: 217–218, fig. 26*d*; Barnard, K. H., 1932: 56–58, fig. 21, pl. 1, fig. 1; Chevreux, 1935: 63–65, pl. 10, figs. 4–6, pl. 11, fig. 10.

TABLE 3

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Rhachotropis natator*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
600–900	4	0	0
900–1100	3	3	100
Day			
600–900	11	6	54.5
900–1100	8	6	75

Eurythenes obesus Shoemaker, 1956: 177–178; Barnard, J. L., 1961: 38–39, fig. 8.

A total of 6 specimens of this species was recovered from 5 samples ranging in depth from 685 to 1000 m. The possibility of demersal activity was suggested by Barnard (1961: 26). He reported that *Eurythenes obesus* had been taken in both pelagic and benthic samples, stipulating the possibility of benthic gear capturing pelagic organisms. The individuals recovered in this present study were certainly many meters above the bottom. Gut analyses revealed debris and what appeared to be silicious sponge spicules which may indicate benthic feeding. If this species does feed on the bottom it must migrate vertically some 500 to 600 m, as indicated by the capture depths and the fact that the floor of the Santa Catalina Basin is at a depth of 1436 m.

Paracallisoma coecus (Holmes)

Scopelocheirus coecus Holmes, 1908: 500–502, figs. 10–12; Barnard, J. L., 1954*a*: 54, pls. 4–5.

Paracallisoma coecus Barnard, J. L., 1954*b*: 57.

This species, known only from the waters off the coast of southern California, occurred in 14 samples from depths ranging from 520 to 1100 m. A total of 56 individuals was recovered from quantitative samples. J. L. Bar-

TABLE 4

Day and Night Depth Distributions for *Paracallisoma coecus*

Depth in meters	Total no. samples	No. positive samples	Per cent positive
Night			
500–900	11	2	18
900–1100	3	2	66
Day			
500–900	16	4	25
900–1100	8	6	75

nard (1954*a*:54) reported a depth-range of from 654 to 1,030 fathoms (1196 to 1884 m) for this species. All of the individuals collected in this present study were from shallower depths (520–1100 m).

Some evidence exists that *Paracallisoma coecus* moves upward during the daylight hours. Table 4 shows that the relative abundance of this species was greater during the daytime, suggesting that some of the population was residing at depths greater than those sampled during this study. This suggestion is also supported by the depth records stated by Barnard.

This species was scarce from depths of less than 900 m. The average number per trawl hour in the five positive samples from depths less than 900 m was 5, while this value for the nine positive samples taken deeper than 900 m was 36.

Cyphocaris anonyx Boeck

Cyphocaris micrononyx Stebbing, 1888: 656, pl. 16.

Cyphocaris anonyx Boeck, 1871: 104–105; Schellenberg, 1926: 210–212, figs. 2*b*, 5*a–b*, pl. 5, fig. 2; Shoemaker, 1945: 187, figs. 1*a–b*; Barnard, J. L., 1954*a*: 53; Waterman, 1939: 256–279.

A total of 115 individuals was recovered from quantitative samples during this study.

Shoemaker (1945:187) recorded this species at depths of from 600 to 1,000 fathoms (1161 to 1935 m), and a single specimen was reported by J. L. Barnard (1954*a*:53) taken in a net tow from 560 to 640 fathoms (1084 to 1239 m). Waterman et al. (1939:268) reported *Cyphocaris anonyx* taken at depths of from about 200 to 1000 m. This present study revealed individuals of this species in 27 samples at depths of from 150 to 1100 m. Waterman also recorded a large portion of the population moving from 600 m in the daytime to about 200 m at night. Some evidence for this migration is found in the capture times and depths of this present study, but it is not conclusive.

Cyphocaris richardi Chevreux

Cyphocaris Richardi Chevreux, 1905: 1–5, figs. 1–2; Chevreux, 1916:1.

Cyphocaris richardi Schellenberg, 1926:206–209, figs. 2*a*, 3*a–e*, 4*a–d*, pl. 5, fig. 1; Barnard, K. H., 1932:35; Stephensen, 1933:4–5; Shoemaker, 1945:187–189, fig. 1*d*; Barnard, J. L., 1954*a*:54, pls. 2–3; Barnard, J. L., 1961:32; Barnard, J. L., 1962:24; Bernstein and Vinogradov, 1955:212–213, figs. 2–3; Bernstein and Vinogradov, 1958:221.

Collected in 28 trawls, a total of 193 individuals was taken in quantitative aliquots. Positive samples ranged in depth from 500 to 1100 m. Table 5 illustrates the day and night depth distributions for *Cyphocaris richardi*. From these data it can be seen that this species was rather evenly distributed between 500 m and the depth of the deepest samples taken (1100 m). There is no conclusive evidence of any vertical movement.

Suborder Hyperiidea

Family Platyscelidae

Platyscelus serratulus Stebbing

Platyscelus serratulus Stebbing, 1888:1470; Stephensen, 1925:215–218, chart 31; Chevreux and Fage, 1925:422, fig. 414; Barnard, K. H., 1930:437; Pirlot, 1930:37; Barnard, K. H., 1932:298; Shoemaker, 1945:259; Hurley, 1956:21–22.

Platyscelus serratulus occurred in 6 samples during this study, a total of 8 specimens was recorded at depths ranging from 170 to 927 m. Stephensen (1925:215–218) reported finding this species at the surface at night. Although only a few individuals were taken dur-

TABLE 5

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Cyphocaris richardi*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
500–900	11	6	55
900–1100	3	3	100
Day			
500–900	16	12	75
900–1100	8	7	88

ing this present study, there is some evidence of a vertical movement toward the surface during the dark hours. The report by Stephensen and the depth and time records presented by Hurley (1956:21–22) support this suggestion.

Family PRONOIDAE

Eupronoe minuta Claus

Eupronoe minuta Stephensen, 1925:160–161, figs. 55–56; Chevreux and Fage, 1925: 425–426, fig. 417; Pirlot, 1929:148–149; Barnard, K. H., 1930:426; Pirlot, 1930:34–35; Barnard, K. H., 1932:289; Shoemaker, 1945: 245–246; Hurley, 1956:19.

A total of 322 individuals of this species was taken from quantitative samples. It was present in 41 trawls ranging in depth from 50 to 1100 m. Table 6 illustrates the day and night depth distributions. *Eupronoe minuta* was one of the two species common at depths of less than 100 m during the daylight hours. The greatest concentrations of individuals were noted from about 50 to 200 m during the day; the rest of the population was rather evenly distributed throughout the depth range of the sampling program. The reason for the apparent absence of individuals between 400 and 500 m is not clear. The nighttime depth distribution shows an obvious massing of the population in the surface waters. Data gathered with the Foxton closing device indicate that the deep, positive, night samples are probably the result of contamination from upper layers as the net was being lowered and raised. This does not exclude the possibility, however, that this species may descend during the dark hours.

Family PHROSINIDAE

Primno macropa Guerin

Euprimno macropa Stephensen, 1924:143–146, chart 22; Pirlot, 1929:130–131; Pirlot, 1930:22.

Primno macropa Barnard, K. H., 1930:424–425; Barnard, K. H., 1932:287–288; Thorsteinson, 1941:93–94, pl. 9, figs. 98–102; Mackintosh, 1934:90, fig. 20; Shoemaker, 1945:234–236; Hurley, 1956:17–18.

This species occurred in 40 samples ranging in depth from 80 to 980 m. A total of 315 individuals was recovered from aliquots of quantitative samples.

Mackintosh (1934:90) offered data which suggest that *Primno macropa* migrates to the surface during the daylight hours and moves

TABLE 6

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Eupronoe minuta*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	1	25
50–100	2	2	100
100–200	7	4	57
200–300	4	0	0
300–400	6	4	66
400–500	2	0	0
500–600	7	0	0
600–700	2	2	100
700–800	1	0	0
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	1	50
50–100	2	2	100
100–200	2	2	100
200–300	4	2	50
300–400	4	3	75
400–500	5	0	0
500–600	5	3	60
600–700	4	3	75
700–800	3	2	66
800–900	4	2	50
900–1100	8	5	62

deeper at night. His study was conducted in Antarctic waters. The present study, however, gives evidence that this species undergoes a typical migratory activity toward the surface at night and retreats to deeper water during the day (Table 7). The daytime depth range was from 200 to 980 m and the nighttime range was from 80 to 650 m. The deep, positive, night samples probably indicate a descent of part of the population during the dark hours.

Family CYSTISOMIDAE

Cystisoma fabricii Stebbing

Thaumatops fabricii Stephensen, 1918:63–64, figs. 22–23; Pirlot, 1929:89.

Cystisoma fabricii Stebbing, 1888:1333; Barnard, K. H., 1932:272–273; Hurley, 1956:10.

A total of 31 individuals was collected from 19 samples ranging in depth from 275 to 1100 m. There is some evidence that this species rises toward the surface at night but this is speculative due to the small number of individuals collected.

TABLE 7

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Primno macropa*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	0	0
50–100	2	2	100
100–200	7	4	57
200–300	4	1	25
300–400	6	3	50
400–500	2	2	100
500–600	7	3	43
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	2	50
400–500	5	3	60
500–600	5	3	60
600–700	4	1	25
700–800	3	2	66
800–900	4	2	50
900–1100	8	4	50

Cystisoma pellucidum (Suhn)

Thaumatops pellucida Stephensen, 1918:64–66, figs. 19, 24–27.

Cystisoma pellucidum Barnard, K. H., 1932:272; Thorsteinson, 1941:92–93; Hurley, 1956:10.

Four individuals of this species were taken in 4 samples ranging in depth from 275 to 468 m. Although vertical movements are suspected for *Cystisoma pellucidum,* the data are too scant to support the suggestion.

Family OXYCEPHALIDAE

Calamorhynchus pellucidus Streets

Calamorhynchus rigidus Stebbing, 1888:1600, pl. 206; Bovallius, 1890:74; Stephensen, 1925:189–191.

Calamorhynchus pellucidus Streets, 1878:285, pl. 2, fig. 5; Bovallius, 1890:73–74, pl. 2, figs. 14–15; Fage, 1960:31–37, figs. 19–20.

This is the first record of this species from Pacific North America. Only 1 specimen was collected during this study, at a depth of 360 m. Although vertical migration is suspected from analysis of earlier works, no conclusions can be drawn here.

Oxycephalus clausi Bovallius

Oxycephalus clausi Bovallius, 1890:60, figs. 4, 7, 8, 22, 54, 65, pl. i, figs. 19–24, pl. ii, fig. 1; Stephensen, 1925:188, chart 27; Barnard, K. H., 1930:433; Barnard, K. H., 1932:294; Fage, 1960:20–21.

This is the first record of this species from Pacific North America. Two individuals were taken at depths of 360 and 520 m. Earlier work suggests a migration toward the surface at night.

Streetsia challengeri Stebbing

Streetsia pronoides Bovallius, 1890:34, pl. III, figs. 7–12, p. 23, fig. 9, p. 35, fig. 62; Pirlot, 1938:360; Hurley, 1956:18–19.

TABLE 8

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Streetsia challengeri*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	2	50
50–100	2	2	100
100–200	7	4	59
200–300	4	2	50
300–400	6	0	0
400–500	2	0	0
500–600	7	0	0
600–700	2	1	50
700–800	1	0	0
800–900	1	1	100
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	4	100
400–500	5	2	40
500–600	5	2	40
600–700	4	1	25
700–800	3	0	0
800–900	4	2	50
900–1100	8	3	37

Streetsia challengeri Stebbing, 1888:1603–1606, pl. 207; Stephensen, 1925:194–199, fig. 75; Pirlot, 1929:164–165; Barnard, K. H., 1930:435; Barnard, K. H., 1932:295; Shoemaker, 1945:255; Fage, 1960:51–63, figs. 36–43.

This species was captured in 31 trawls at depths of from 10 to 1100 m. A total of 67 individuals was sorted from pint aliquots of the quantitative samples.

There is definite evidence of diurnal migration toward the surface at night (Table 8). Results of sampling with the Foxton device indicate that the two positive, deep, nighttime samples were probably the result of contamination from shallower depths.

Family HYPERIIDAE

Hyperia spinigera Bovallius

Hyperia spinigera Barnard, K. H., 1932: 273–274, fig. 160; Thorsteinson, 1941:87–88, pl. 8, figs. 79–82; Shoemaker, 1945:238, fig. 35; Hurley, 1956:15.

Eight individuals of this species were taken in 5 samples at depths of from 300 to 954 m. Although only a few specimens were recovered, there is some evidence of vertical movement upward at night.

Hyperia bengalensis (Giles)

Hyperia bengalensis Shoemaker, 1942:49; Shoemaker, 1945:238; Hurley, 1956:15–16.

Some taxonomic confusion accompanies this species; Hurley (1956:15–16) gives an account of the systematics. The specimens collected in this present study are very similar to that pictured by Stebbing (1888) as *H. schizogeneios.*

This species was collected in 13 samples ranging in depth from 85 to 975 m. A total of 52 individuals was sorted from quantitative aliquots. There is definite evidence that *Hyperia bengalensis* moves toward the surface at night. Its daytime depth range was from 288 to 975 m, while at night it was collected from 85 to 650 m.

Hyperia galba (Montague)

Hyperia galba Sars, 1895:7, pl. 2, fig. 1; Calman, 1898:265; Stephensen, 1924:81, chart 11; Barnard, K. H., 1932:273.

Hyperia galba was collected in 31 trawls at depths of from 85 to 1100 m, and 78 individuals were taken from pint aliquots of quantitative samples.

The data shown in Table 9 indicate an obvious migration toward the surface at night, concentrating at depths of less than 500 m.

Family VIBILIIDAE

Vibilia armata Bovallius

Vibilia armata Chevreux and Fage, 1925: 387–388, fig. 391; Pirlot, 1929:100–101; Pirlot, 1930:11; Barnard, K. H., 1930:104; Barnard, K. H., 1932:264–265; Hurley, 1956: 10–11.

This species was found in 54 samples at depths of from 10 to 1100 m. A total of 2,742

TABLE 9

Day and Night Depth Distributions for *Hyperia galba*

Depth in meters	Total no. samples	No. positive samples	Per cent positive
Night			
0–50	4	0	0
50–100	2	1	50
100–200	7	2	28
200–300	4	4	100
300–400	6	3	50
400–500	2	1	50
500–600	7	1	13
600–700	2	0	0
700–800	1	0	0
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	1	25
300–400	4	4	100
400–500	5	2	40
500–600	5	3	60
600–700	4	0	0
700–800	3	2	75
800–900	4	1	25
900–1100	8	6	75

TABLE 10

Day and Night Depth Distributions for *Vibilia armata*

Depth in meters	Total no. samples	No. positive samples	Per cent positive
Night			
0–50	4	3	75
50–100	2	2	100
100–200	7	5	70
200–300	4	3	75
300–400	6	5	82
400–500	2	2	100
500–600	7	2	30
600–700	2	2	50
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	3	75
300–400	4	2	50
400–500	5	4	80
500–600	5	5	100
600–700	4	2	50
700–800	3	2	66
800–900	4	3	75
900–1100	8	7	88

individuals was noted in quantitative aliquots.

The data suggest that *Vibilia armata* exists in a thick zone ranging from the surface to about 800 m at night and from 200 to 1100 m during the day. It is probable that the lower, daytime depth limit was greater than the sampling program of this study. Table 10 illustrates the depth distributions. It appears that the entire population moves upward some 200 m at night without actually concentrating near the surface.

Vibilia viatrix Bovallius

Vibilia californica Holmes, 1908:490–492, figs. 1–2.

Vibilia viatrix Stephensen, 1918:41–43, fig. 13; Chevreux and Fage, 1925:385–386, fig. 390; Pirlot, 1929:95–96; Barnard, K. H., 1930:403; Pirlot, 1930:10–11; Barnard, K. H., 1932:262–263; Shoemaker, 1945:234, Hurley, 1956:11.

Individuals of this species were taken in 53 trawls ranging in depth from 10 to 1100 m. A total of 658 specimens was recovered from pint aliquots. A few individuals associated with salps were noted on the surface.

Table 11 illustrates the day and night depth distributions. This species displayed a unique pattern of vertical migration: the upper portions of the population remained rather stable, while the deeper dwelling members rose at night, resulting in an absence of individuals at great depths during the dark hours.

Family Phronimidae

Phronima sedentaria (Forskal)

Phronima sedentaria Holmes, 1908:490; Stephensen, 1924:114–121, figs. 50–51, chart 15; Chevreux and Fage, 1925:393–395, fig. 396; Pirlot, 1929:110–112; Barnard, K. H., 1930:422; Pirlot, 1930:12–14; Barnard, K. H.,

TABLE 11

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Vibilia viatrix*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	4	100
50–100	2	1	50
100–200	7	4	57
200–300	4	3	75
300–400	6	4	66
400–500	2	2	100
500–600	7	1	14
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	0	0
Day			
0–50	2	2	100
50–100	2	1	50
100–200	2	1	50
200–300	4	1	25
300–400	4	4	100
400–500	5	4	80
500–600	5	4	80
600–700	4	2	50
700–800	3	3	100
800–900	4	3	75
900–1100	8	7	87

TABLE 12

DAY AND NIGHT DEPTH DISTRIBUTIONS FOR *Phronima sedentaria*

DEPTH IN METERS	TOTAL NO. SAMPLES	NO. POSITIVE SAMPLES	PER CENT POSITIVE
Night			
0–50	4	0	0
50–100	2	2	100
100–200	7	7	100
200–300	4	2	50
300–400	6	4	66
400–500	2	0	0
500–600	7	3	47
600–700	2	2	100
700–800	1	1	100
800–900	1	0	0
900–1100	3	2	75
Day			
0–50	2	0	0
50–100	2	0	0
100–200	2	0	0
200–300	4	4	100
300–400	4	4	100
400–500	5	4	80
500–600	5	4	80
600–700	4	2	50
700–800	3	2	75
800–900	4	2	50
900–1100	8	6	75

1932:283–284; Thorsteinson, 1945:236; Hurley, 1956:16.

Phronima sedentaria was collected in 53 trawls at depths of from 80 to 1100 m. A total of 575 individuals was sorted from quantitative aliquots.

During the daytime this species was found at depths ranging from about 275 to 1100 m, with the greatest concentrations noted above 400 m. There was a distinct rise of the population toward the surface at night (Table 12). The deep, positive samples at night may be the result of either a descent during the dark hours or the presence of a nonmigrating portion of the population residing below the depth of perceivable light. There is also the probability of some contamination from shallower depths.

It has been suggested in much of the earlier literature that only the young of this species were ever captured near the surface and that the adults were typically taken in deep trawls. Mean size records obtained during this present study showed no difference in age groups for individuals captured above and below a depth of 100 m.

Family PARAPHRONIMIDAE

Paraphronima gracilus Claus

Paraphronima gracilus Stephensen, 1924: 75–77; Chevreux and Fage, 1925:391, fig. 394; Pirlot, 1929:104–105; Barnard, K. H., 1932: 267; Hurley, 1956:12–13.

Paraphronima gracilus was taken in 49 trawls ranging in depth from 80 to 1100 m. A total of 472 individuals was sorted from pint aliquots.

The greatest concentrations of individuals during the daylight hours were found at depths of from 275 to 400 m. This species occurred

TABLE 13

Day and Night Depth Distributions for *Paraphronima gracilus*

Depth in meters	Average no. per trawl hour	Per cent positive samples
Night		
0–400	72	83
400–1100	15	37
Day		
0–400	44	38
400–1100	28	82

in a great number of samples and contamination is suspected in certain deep night trawls. Density variations, however, support evidence of an ascent toward the surface during the dark hours. Table 13 shows the average numbers per trawl-hour for the positive samples, and the percentages of positive stations at different depth ranges during the day and night.

Paraphronima crassipes Claus

Paraphronima crassipes Stephensen, 1924: 77–78; Chevreux and Fage, 1925:390–391, figs. 393–394; Pirlot, 1929:105–106; Barnard, K. H., 1930:409–410; Barnard, K. H., 1932: 267–268; Shoemaker, 1945:234; Hurley, 1956: 13.

Specimens of this species were found in 54 samples ranging in depth from 80 to 1100 m. A total of 922 individuals was sorted from pint aliquots. A movement toward the surface at night was apparent (Table 14).

SUMMARY

This study treats 5 species of the suborder Gammaridea and 16 species of the suborder Hyperiidea collected from the waters off the coast of southern California. Two additional genera (*Scina* and *Orchomenella*) were collected, but are not discussed here because of problems in specific identification. Two species of the family Oxycephalidae (*Oxycephalus clausi* and *Calamorhynchus pellucidus*) not previously reported from California waters were taken during this study, raising the known number of local pelagic hyperiids from 43 to 45.

With the exception of *Cyphocaris anonyx,* all of the gammarids were noted to be deep-living forms common only in samples taken at depths greater than about 650 m. There appear to be diurnal movements in some species, involving a rise during the daylight hours and a sinking at night. The controlling factors here are not clear, and may involve an endogenous rhythm.

With the exception of a few species, the upper depth limit of the hyperiids was defined by the thermocline, and captures were uncommon at depths of less than 50 m. From repeated sampling and analysis of abundance, it was found that most of the hyperiids exist in a thick band down to depths greater than 1000 m during the daytime, with the greatest concentrations recorded between 200 and 600 m. Most of these species rise to shallower levels during nightly migrations toward the surface.

Although it is easy to speculate on the advantages of such vertical movements, it is very difficult to establish the actual causes. The results of this study indicate that, in addition to the barrier imposed by the thermocline, light is the most important factor influencing the migrations of the hyperiids. The controlling effect of light intensity is illustrated by the massing of populations at shallow levels during periods of dim light and by the vertical spreading-out of individuals at times of total darkness.

A great deal of work remains to be done on midwater ecology in general. The use of more refined sampling methods will enable workers to establish accurate depth distributions and will offer more precise information on the habits of vertical movements.

TABLE 14

Day and Night Depth Distributions for *Paraphronima crassipes*

Depth in meters	Per cent positive day samples	Per cent positive night samples
0–200	0	50
200–1100	75	65

REFERENCES

ARON, W., N. RAXTER, R. NOEL, and W. ANDREWS. 1964. A description of a discrete depth plankton sampler with some notes on the towing behavior of a 6-foot Issacs-Kidd midwater trawl and a one-meter ring net. Limnology and Oceanography 9(9):324–333.

BARNARD, J. L. 1954*a*. Four species of bathypelagic Gammaridea (Amphipoda) from California. Alan Hancock Foundation Occas. Papers 13:52–69.

——— 1954*b*. Marine Amphipoda from Oregon. Oregon State Monographs 8, 103 pp.

——— 1957. New bathypelagic amphipods of the genera *Rhachotropis* and *Lepechinella* with keys to the genera. Bull. S. Calif. Acad. Sci. 56:(1):14–20.

——— 1961. Gammaridean Amphipoda from depths of 400 to 6000 meters. Galathea Rept. 5:23–128.

——— 1962. South Atlantic abyssal amphipods. Reprint from: Abyssal Crustacea, pp. 1–76. Columbia Univ. Press, N.Y.

BARNARD, K. H. 1930. Amphipoda. British Antarctic ("Terra Nova") Expedition, 1910–1913. Natural History Rept., Zoology 8(4): 307–454.

——— 1932. Amphipoda. Discovery Rept. 5:1–326.

BERNSTEIN, J. A., and M. VINOGRADOV. 1955. Pelagicheskie gammaridy (Amphipoda-Gammaridea) Kurilo-Kamchatskoj Vpadiny. Akad. Nauk USSR, Trudy Inst. Okean. 12:210–287.

——— 1958. Pelagicheskie gammaridy (Amphipoda - Gammaridea) Severo - Zapandoj Chasti Tixogo Okean, Akad. Nauk USSR, Trudy Inst. Okean. 27:219–257.

BOECK, A. 1871. Crustacea Amphipoda Borealia et Arctica. Fohr. (Nordske) Vidensk.-Selsk. (1870), pp. 83–280.

BOVALLIUS, C. 1890. The Oxycephalids. Societas Scientiarum-Upsala, Nova Acta, Ser. 3, 14:1–141.

CALMAN, W. T. 1898. On a collection of Crustacea from Puget Sound. Ann. N. Y. Acad. Sci. 11(13):259–284.

CHEVREUX, E. 1905. Description d'un amphipode (*Cyphocaris richardi* nov. sp.) provenant des pêches au filet ouverture de la dernière campagne du yacht "Princess-Alice" (1904). Bull. Oceanogr. Inst. Monaco 24: 1–5.

——— 1916. Sur les amphipodes du genre *Cyphocaris* Boeck recueillis par la "Princess-Alice" au moyen du filet Richard à grande ouverture. Bull. Oceanogr. Inst. Monaco 319:1–7.

——— and L. FAGE. 1925. Amphipodes. In: Faune de France, Vol. 9, pp. 1–488. Lechevalier, Paris.

EMERY, K. O. 1960. The Sea off Southern California. John Wiley and Sons, New York.

FAGE, L. 1960. Oxycephalidae, amphipodes pelagiques. The Carlsberg Foundation's Oceanographic Expedition Round the World 1928–30 and Previous "Dana" Expeditions. Dana-Rept. 52:1–145.

HOLMES, S. J. 1908. The Amphipoda collected by the U. S. Bureau of Fisheries steamer "Albatross" off the west coast of North America in 1903 and 1904, with descriptions of a new family and several new genera and species. Proc. U. S. Natl. Mus. 35:489–543.

HURLEY, D. E. 1956. Bathypelagic and other Hyperiidea from California waters. Allan Hancock Foundation Occas. Papers 18:1–25.

——— 1963. Amphipoda of the family Lysianassidae from the west coast of North and Central America. Allan Hancock Foundation Occas. Papers 25:1–160.

ISSACS, J. D., and L. W. KIDD. 1953. Issacs-Kidd Midwater Trawl. Scripps Inst. of Oceanogr. Ref. 53-3:1–21.

MACKINTOSH, N. A. 1934. Distribution of macroplankton in the Atlantic sector of the Antarctic. Great Britain Discovery Rept. 9:67–160.

PIRLOT, J. 1929. Les Amphipodes Hyperiides. (Res. Zool. de la Croisière Atlantique de l' "Armauer Hansen.") Vol. 1, pp. 1–196. Univ. de Liege, Trav. de l'Inst. Ed van Beneden, Bruxelles.

——— 1930. Les Amphipodes de l'Expedition du Siboga, Part I. Les Amphipodes Hyperiides. Siboga-expeditie, Monogr. 33a:1–54.

SARS, G. O. 1895. An account of the Crustacea of Norway, Vol. I. Amphipoda.

Schellenberg, A. 1926. Amphipoda 3: Die Gammariden der deutschen Tiefsee-Expedition. Wiss. Ergeb. Deutschen Tiefsee Exped. "Valdivia" (1898–1899) 23:195–243.

Shepard, F. P., and K. O. Emery. 1941. Submarine Topography off the California Coast: Canyons and Tectonic Interpretations. Geol. Soc. Am. Special Papers 31, 171 pp.

Shoemaker, C. 1942. Amphipoda crustaceans collected on the Presidential Cruise of 1938. Smithsonian Misc. Coll. 101(11):1–52.

——— 1945. The Amphipoda of the Bermuda Oceanographic Expeditions, 1929–1931. Zoologica 29–30:185–272.

——— 1956. Notes on the amphipods *Eurythenes gryllus* (Lichtenstein) and *Katius obesus* Chevreux. Proc. Biol. Soc. Washington 69:177–178.

Stebbing, T. T. R. 1888. Report on the Amphipoda collected by H.M.S. "Challenger" during the years 1873–1876. In: The Voyage of H.M.S. "Challenger," Zoology, Vol. 29.

Stephensen, K. 1918. Hyperiidea-Amphipoda (part 1), D, 2. Report on the Danish Oceanographical Expeditions 1908–1910 to the Mediterranean and Adjacent Seas. Vol. II, Biology, C–D, 3, pp. 3–70.

——— 1924–25. Hyperiidea-Amphipoda (parts 2–3), D, 4. Ibid. Vol. II, Biology, D, 4–6, pp. 71–252.

——— 1933. Amphipoda of the Godthaab Expedition 1928 (Denmark). Medd. Groenl. 79(7):1–88.

Thorsteinson, E. D. 1941. New or noteworthy amphipods from the North Pacific coast. Univ. Washington Publ. Oceanogr. 4(2):50–94.

Watermann, T., R. Nunnemacher, F. Chace, and G. Clarke. 1939. Diurnal vertical migrations of deep-water plankton. Biol. Bull. 76:256–279.